Title: The relative value of field survey and remote-sensing for biodiversity assessment

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Summary

1. The importance of habitat for biodiversity is well established but the two most commonly used methods to measure habitat (field survey and remote-sensing) have seldom been explicitly compared.

2. We compare high resolution sample-based field survey (Countryside Survey) with medium resolution remote-sensed habitat data (the highest resolution of Land Cover Map available) for Great Britain. Variation in abundance of 60 bird species from 335 1 km squares was modelled using habitat predictors from the two methods. Model comparisons assessed the explanatory power of (a) field survey versus remote-sensed data and (b) coarse information on habitat areas (Broad Habitats) versus fine grained information on Landscape Features.

3. Field survey data (combining Broad Habitat and Landscape Feature predictors) explained more variation in bird abundance than remote-sensed data (comprising Broad Habitat predictors only) for 57 species and had significantly higher mean explanatory power, averaged across 60 species models. The relative explanatory power of remote-sensing, as a proportion of that provided by field data, was measured at 73%, averaged across 60 species models. Predictions from field survey Broad Habitat data were more accurate than those from either remote-sensed Broad Habitat data, or field survey Landscape Feature data, averaged across 60 species models.

4. High resolution data generate more reliable models of predicted local population responses to land use change than lower resolution remote-sensing data. Collection of field data is typically costly in time, labour and resources, making use of remote-sensing more feasible for assessment at larger spatial extents if data of equivalent value are produced, but the cost-benefit threshold between the two is likely to be context-specific. However, integration of field survey with remote-sensed data provides accurate predictions of bird distributions, which suggests that both forms of data should be considered for future biodiversity surveys.

Key-words:

Bird abundance, Broad Habitats, habitat association modelling, land use survey methods, landscape composition, landscape features, predictive model, spatial resolution

Introduction

Land-use is a major factor influencing biodiversity (Benton, Vickery, & Wilson 2003; Foley *et al.* 2005), making land-use change (through impacts to land cover in natural and human-modified landscapes) an important potential driver of species' declines (Butchart *et al.* 2010). Identification of land-use impacts on biodiversity requires spatially and temporally matched data on habitat and species distributions (Kerr & Ostrovsky 2003; Turner *et al.* 2003; Rose *et al.* 2014). Biodiversity-habitat association studies are likely to be most informative for environmental management when examining relationships at high resolution (where the minimum area of habitat units measured is low, therefore giving fine spatial grain), but over large geographic areas (Whittingham *et al.* 2007; Brambilla *et al.* 2009; Rose *et al.* 2014). Analyses of this type have the potential to reflect assemblage responses to habitats at multiple scales (Blackburn & Gaston 2002), including scales relevant both biologically and for management administration (Mattison & Norris 2005). Despite this, pragmatic trade-offs result in a tendency for high resolution biodiversity-habitat analyses to cover relatively small areas (Whittingham *et al.* 2005), while larger scale (hereafter meaning 'spatial extent') studies typically have lower resolution (Siriwardena, Cooke, & Sutherland 2011; Rose *et al.* 2014). Funding limitations favour cost-effective solutions to habitat data requirements. Improved understanding of the comparative strengths and weaknesses of alternative forms of habitat data available at national scales would facilitate optimal resource allocation for research (Kerr & Ostrovsky 2003; Turner *et al.* 2003; Rose *et al.* 2014).

We compared high resolution (hereafter meaning resolution in terms of both spatial grain and habitat classification), nationally representative field survey data for Great Britain (Countryside Survey 2000) with lower resolution, remote-sensed data (Land Cover Map 2000), at the same spatial extent, for assessment of bird-habitat associations. The explanatory power of field data and remote-sensed data in models of spatial variation in abundance of 60 bird species across Great Britain was assessed. The design aimed to test and quantify the improvement in predictions generated by field survey data, over and above those yielded using remote-sensed data, as a result of the higher resolution and accuracy of habitat mapping and classification in field survey (Saveraid *et al.* 2001). Such comparisons are rarely possible because field survey (habitats and birds) and remote-sensed habitat data collected at comparable spatial and temporal scales are scarce. The relative value of the two methods for predicting large scale patterns has yet to be assessed (Müller & Brandl 2009).

Field survey has traditionally been the main method of detailed habitat assessment (Rodwell 2006; Fuller 2012), informing about land-use impacts on a variety of taxa (Aviron *et al.* 2005; Whittingham *et al.* 2005). Field survey can be used to record habitat types based on plant species composition and its resolution is limited mainly by human expertise for field measurement of habitats and the effort required. Accurate, high resolution habitat data are produced, but typically demand considerable resources (Kerr & Ostrovsky 2003) and may pose prohibitive logistical challenges at large scales (Müller & Brandl 2009).

Remote-sensing (from satellites or airborne sensors) is developing as a method for habitat assessment with a variety of imagery becoming available (Turner *et al.* 2003; Recio *et al.* 2013; Shirley *et al.* 2013). Large scale remote-sensing data tend to be lower in resolution (Rose *et al.* 2014), while higher resolution sources such as lidar are typically unavailable at national scales (Simonson, Allen & Coombes 2014). Many sources of remote-sensed imagery such as Landsat (Fuller *et al.* 2005; Shirley *et al.* 2013), Google Earth (Hughes, Martin & Reynolds 2011) and lidar (Simonson, Allen & Coombes 2014), are available in raster format, which requires considerable processing effort to produce vector (polygon) formats suitable for analysis. Novel remote-sensed imagery has great potential for use in biodiversity modelling, but methods to convert raw pixel information into usable data on habitats or management require development (Shirley *et al.* 2013; Shereen, Bonthoux & Balent 2014). Here we use Land Cover Map 2000, which has a resolution of >0.5 ha, because bird data and field data were available for the same period.

Remote-sensing at large scales may be more cost-effective than field survey for timely collection of large scale habitat data (Gould 2000; Kerr & Ostrovsky 2003; Turner *et al.* 2003; Fuller *et al.* 2005), but tends to result in lower spatial resolution than field survey, being constrained by the pixel size of the imagery used and the lack of spectral difference between particular habitat types (Kerr & Ostrovsky 2003; Turner *et al.* 2003). Habitat classification by remote-sensing is indirect (based on reflectance of lasers or light) and spectral confusion can reduce accuracy (Kerr & Ostrovsky 2003; Turner *et al.* 2003). We hypothesised that field data, highly resolved in both spatial grain and habitat classification, would better predict bird abundance than lower resolution remote-sensing.

Broad classifications of habitat at the field scale (hereafter referred to as Broad Habitats), including land cover categories of human-modified (e.g. arable), semi-natural (e.g. dwarf shrub heath), and natural (broadleaved woodland) landscapes, are routinely collected by both field survey and remote-sensing (Howard *et al.* 2003; Morton *et al.* 2011). Features of habitat measured at high resolution (referred to here as Landscape Features) including hedges and individual trees (trees outside typical woodland habitat), are recorded by field survey but, although raster photographic data frequently capture images of both hedges and individual trees, interpretation to identify them has yet to be done for Great Britain (Tebbs & Rowland 2014). The inclusion of Landscape Features is one factor contributing to the high resolution of field surveys relative to some large scale remote-sensing products. Broad Habitats typically cover a larger proportion of land surface area than Landscape Features (Fuller *et al.* 2002; Firbank *et al.* 2003). Broad Habitat definitions may incorporate information on multiple habitat types, for example broadleaved woodland describes a guild of tree species, but do not discriminate features including characteristic understory flora, woodland rides and glades, which may be important components of a habitat matrix. Conversely, the integration of such features as a broad habitat may actually be more critical for breeding birds. We hypothesised that Broad Habitats would be more important for determining bird abundance than Landscape Features (Siriwardena, Cooke, & Sutherland 2011).

This article tests the following hypotheses about how data perform in predicting spatial variation in bird abundance:

1. High resolution field data will outperform lower resolution remote-sensed data, due to the combined effects of more accurate Broad Habitat data from field survey and the inclusion of Landscape Features as additional variables unavailable in the remote-sensed data.
2. Broad Habitats (from field data or remote-sensing) will outperform Landscape Features (from field data).

The outcomes will provide valuable information on the advantages and constraints of the use of different data types for collecting data and for constructing predictive models in order to make objective decisions about landscape management.

Materials and methods

DATA

Field Survey Habitats (Countryside Survey)

Field data on total land cover (including Broad Habitats and Landscape Features) were collected across a randomly selected, stratified by land class, sample of 569 1km squares, targeting rural land in Great Britain in 1998/1999 as part of Countryside Survey 2000 (Howard *et al.* 2003). A subset of data from 335 squares, where breeding bird surveys took place, was used for the current analysis (see *Breeding bird survey* and *Bird abundance response variables* below)**.** Field surveyors mapped and described land cover by combinations of points, lines and polygons, at a scale of approximately 1:5500 (Howard *et al.* 2003), identifying land cover for every parcel within the square. All features present in non-urban areas above minimum length (<20m), area (0.04 ha) and point (individual trees diameter at breast height >5cm) criteria were mapped. The Broad Habitat classification was based on hierarchical nomenclature corresponding to Joint Nature Conservation Committee (JNCC) Broad Habitats, which encompasses the entire range of UK habitats (Jackson 2000; Howard *et al.* 2003; Norton *et al.* 2012).

Remote-sensed Habitats (Land Cover Map)

Remote-sensed land cover data were obtained from Land Cover Map 2000, a UK-wide, satellite-based survey (Fuller *et al.* 2002). Land cover was derived from satellite scenes recorded during 'winter' (October 1997 to April 1998) and 'summer' (mid-May to August 1998) periods. The main sensor was Landsat, which identified coarse segments (>0.5 ha). Interpretative work trained a computer classification system to assign polygons to '22 classes based on Broad Habitats' (Jackson 2000; Fuller *et al.* 2002). Landscape Feature data were not available from remote-sensing. Data were extracted for the 335 1km squares for which contemporaneous field data were available, allowing direct comparison between the datasets.

Habitat Predictor Variables

A subset of habitat variables were considered for inclusion in models based on *a priori* knowledge of habitats predicted to influence breeding birds (Siriwardena, Cooke, & Sutherland 2011). The subset comprised 15 of 27 classes based on Broad Habitats available in both field data and remote-sensing: broadleaved/mixed woodland, coniferous woodland, arable and horticulture, improved grassland, neutral grassland, calcareous grassland, acid grassland, bracken, dwarf shrub heath, fen marsh swamp, bog, standing open water and canals, montane habitats, inland rock, built up areas and gardens (Table S1). Two Broad Habitats were not considered: 'boundary and linear features' (due to lack of data and inconsistencies in recording) and 'rivers and streams' (remote-sensed data for this category could not be distinguished from the Broad Habitat 'standing open water'). The habitat classification ‘sea’ was used as a proxy for any of the ten coastal habitat classifications to make the study tractable. The Landscape Features considered were drawn from the variables available in the field data, where these matched habitats described as important for birds in the literature (Table S1 displays the variables used for 60 species analyses). To avoid inclusion of large numbers of predictor variables for which sample sizes were low, Landscape Features were considered for inclusion only if they were present in 10% or more of the 335 squares sampled. Landscape Features considered included linear (bank, ditch, dry stone wall, fence, stream, woody linear feature) and point (pond, scrub, tree) features. Three Landscape Feature composites, ‘woody linear feature’ (hedges, lines of trees and belts of trees), ‘ditch’ (roadside ditches and other ditches) and ‘bank’ (stone and earth banks), were considered (see *'Hypotheses'* below, Cramp and Simmons 2006).

For subsequent use as model covariates, habitat and landscape feature variables were summed at the 1km square level as area of cover in m^2 (Broad Habitat areas), the sum of length in metres (linear features) or counts (point features). These values are likely to reflect habitats potentially used by many bird species breeding in the square, given the mobility of birds and typical territory sizes; a 1 km square could be occupied by multiple breeding pairs for the majority of the bird species considered. Potential model covariates, as listed above, were centred by subtracting the sample mean and scaled by dividing by the sample standard deviation (Schielzeth 2010).

Breeding Bird Surveys

Breeding bird surveys were carried out between April and June 2000 on the sample of 335 1km squares for which habitat data were measured (Wilson & Fuller 2002). Bird counts were recorded along transects in three distance bands by skilled contract workers or volunteers (Gregory & Baillie 1998; Wilson & Fuller 2002). Four separate transects were covered per square on each of two visits (April to mid-May and mid-May to June), giving representative coverage of habitats in each square that was more intensive than the two-transect method used in the BTO/JNCC/RSPB Breeding Bird

Survey (Wilson & Fuller 2002). Bird and habitat data were collected as far as possible within a year of one another. Difficulties in obtaining complete imagery in any one year (due to cloud) made mismatches in timing unavoidable. Habitats in some polygons will have changed between years (Norton et al. 2012), particularly in arable areas, but crop rotations are likely to limit changes at the 1km square scale.

Bird Abundance Response Variables

Response variables were individual bird species counts (60 species total, Table 3) for each 1km square. Bird species selected for analysis had the highest non-zero counts for the 335 survey squares, omitting managed species (e.g. ring-necked pheasant *Phasianus colchicus*) and highly colonial species (e.g. rook *Corvus frugilegus*). Carrion crow *Corvus corone* counts included hooded crow *Corvus cornix* counts. Counts were summed across all four transects and distance bands, omitting birds in flight. The maximum count across visits was selected as the observed value for each species at each square (Table S1), aiming to capture breeding numbers at peak detectability for early and late breeders. Relative abundance (observed counts) was modelled, not absolute abundance or density, so not adjusting for imperfect detection. Only one bird dataset was used, the two habitat datasets differed little in gross habitat measures (Fuller *et al.* 2002) and the focus was not on differences between species. Therefore, accounting for detection rather than modelling relative abundance was not expected to change the results (all models for each species would be adjusted by approximately similar constants), but would add unnecessary, potentially problematic complexity (Banks-Leite *et al*. 2014).

Some zero counts may occur where range-restricted bird species do not occur in all regions. To avoid such uninformative (with respect to land-use relationships) zeroes, 1 km squares were excluded from analyses if they occurred in a 10 km national grid square within which no individual of a given species was recorded as present in the 1988-91 breeding bird atlas (Gibbons, Reid & Chapman 1993). The number of squares used for species-specific analyses therefore varied (Table 3).

ANALYSES

Hypotheses

For each bird species, an *a priori* hypothesis regarding habitat influences on abundance was formulated by examining habitat preferences (see Cramp and Simmons 2006). This identified variables to be included as potential predictor variables for each species (see 'Habitat predictor variables', Table S1). All models included a categorical variable identifying squares as lowland or upland, based on Environmental Zones (Wilson & Fuller 2002).

Model structure

Species-specific analyses modelled bird counts as a function of habitat predictors in Generalized Linear Models, with a Poisson error structure and log link function, as is standard for analysis for breeding bird survey data (Siriwardena, Cooke & Sutherland 2011). Negative binomial errors were not used because preliminary analyses revealed unrealistic predicted values for certain bird species in squares with high density of hedges or trees. Five models were generated per species, each of which corresponded to one of five '*Model Types*' differing in the type of habitat predictors and their dataset of origin (Table 1). This allowed comparison of separate models including field data and/or remote-sensed data, and also Broad Habitats and Landscape Feature predictors, as well as the two in combination (hereafter, 'Combined Habitats'). Broad Habitats were available in both datasets, while Landscape Features were available only in field data, so the number of variables compared between models was sometimes unequal. Explanatory power was measured as the percentage of deviance explained by variables from different datasets or groupings. Parsimony was not relevant to the comparison, so deviance was a more appropriate measure than alternatives such as Akaike's Information Criterion. Predictive power was assessed through cross-validation (see below).

Bootstrapped model comparisons

To determine whether there was an overall significant difference in explanatory power between *'Model Types'* across all 60 species, a bootstrapping procedure was adopted. Comparisons between any two *'Model Types'* were made by calculating the within-species difference in explanatory power (defined by percentage deviance explained), then taking the mean of these differences across all species. This provided a clear test statistic against which bootstrap-based samples could be compared. Under the null hypothesis that the two model types show no difference in power, the observed differences across the 60 species were randomly sampled with replacement and then randomly assigned to be negative or positive with equal probability, thus simulating from the null distribution. From this sample, the test statistic was re-calculated by taking the mean across the 60 values and stored. The whole process was repeated 1000 times in order to obtain 1000 values of the test statistic under the null hypothesis. P-values were calculated as the proportion of occurrences of re-sampled mean difference estimates that exceeded the test statistic, thus measuring the probability that the true value of the test statistic was larger.

Goodness-of-fit and cross validation

Practical implications of differences between field data and remote-sensing in prediction were assessed by comparing fitted and observed values for the *'Field Data Combined Habitats'* and *'Remote-sensed Broad Habitat'* model types, the types comprising all available field data and remote-sensed data respectively (Table 3). Mean Absolute Error (MAE) between fitted and observed values was calculated for each species. This was chosen over Mean Square Error because the values are on the same scale as the bird data (i.e. counts per 1km^2). A cross-validation procedure assessed the predictive performance of the datasets. For each species, data were partitioned into a randomly selected training dataset of 80% of squares (rounded to the nearest integer) and a testing dataset comprising the remainder of the squares. Models were fitted to the training data and then used to predict bird counts with the testing dataset and MAE was recalculated.

Results

MODEL PERFORMANCE

Figure 1 displays the mean explanatory power (% deviance explained) across all 60 species for the five *'Model Types'* differing in habitat predictors (Table 2). Mean explanatory power was lowest for species models derived from Landscape Features from field data alone (14%). Broad Habitats explained intermediate amounts of deviance (remote-sensed 24%, field data 28%) but this increased when they were combined with Landscape Features from field data (remote-sensed data 29%, field data 33%; Fig. 1). Figure 2 shows the explanatory power for 60 individual bird species separated into the five *'Model Types'*.

FIELD DATA VERSUS REMOTE-SENSED DATA

In a comparison of all data available, field data outperformed remote-sensed data in predicting bird abundance. *'Field Data Combined Habitats'* had higher explanatory power than *'Remote-sensed Broad Habitats'* for 57 of 60 species (Fig. 2) and significantly higher mean explanatory power across all species (Table 2, Fig. 1). When considering Broad Habitat data alone, field data had higher explanatory power than remote-sensed data for 50 of 60 species (Fig. 2) and significantly higher mean explanatory power across all species (Table 2, Fig. 1). The superior performance of Broad Habitats from field data was enhanced by inclusion of Landscape Features to form Combined Habitats models (Table 2). *'Field Data Combined Habitats'* had higher explanatory power than *'Remote-sensed Combined Habitats'* for 50 of 60 species (Fig. 2) and significantly higher mean explanatory power across all species (Table 2, Fig. 1). The mean improvement in explanatory power of field data over remote-sensed data was greater for Combined Habitats than for Broad Habitats alone (mean difference in percent deviance averaged across 60 species models: Combined Habitats = 3.91, Broad Habitats = 3.89, Table 2).

Differences between field data and remote-sensing for prediction were further assessed by comparing observed and fitted values for the *'Remote-sensed Broad Habitats'* and *'Field Data Combined Habitats'* model types (Table 3). Mean absolute error between fitted and observed values (MAE) averaged across squares demonstrated a closer fit for field data (MAE lower for 51/60 species, MAE averaged across 60 species = 2.76) compared to remote-sensed data (MAE lower for 6/60 species, MAE averaged across 60 species = 2.94, MAE equal for 3/60 species, Table 3). This result was robust to cross-validation, out-of-sample predictions were closer to observed values for field data (MAE lower for 48/60 species, MAE averaged across 60 species = 2.65) compared to remote-sensed data (MAE lower for 9/60 species, MAE averaged across 60 species = 2.88, MAE equal for 3/60 species, Table S2).

BROAD HABITATS VERSUS LANDSCAPE FEATURES

Comparing the two components of the field dataset demonstrated that Broad Habitats outperformed Landscape Features in prediction of bird abundance. *'Field Data Broad Habitats'* had higher explanatory power than *'Field Data Landscape Features'* for 55/60 species, while *'Remote-sensed Broad Habitats'* had higher explanatory power than Landscape Features for 53/60 species (Fig. 2). Broad Habitats from both field data and remote-sensed data had significantly higher mean explanatory power than Landscape features (mean difference in percent deviance averaged across 60 species models: +13.82 for field data Broad Habitats, +9.92 for remote-sensed Broad Habitats Table 2, Fig. 1).

Discussion

Our results support the hypothesis that national-scale field survey data outperform remote-sensed equivalents as predictors of spatial variation in bird abundance, providing more accurate models of breeding bird counts (Figs 1 & 2, Table 2). The explanatory power of remote-sensed data alone, as a percentage of that provided by the Field Data Combined models (which generally had the highest explanatory performance), was 73% (Table 2). The extent to which increases in explanatory power produce better predictions of bird numbers is a key issue. Measures of observed versus fitted values suggest that more reliable predictions of bird numbers are likely to be obtained from field survey data than from remote-sensed data. Examples of more accurate predictions resulting from field data ranged in magnitude from small errors for species such as wheatear *Oenanthe oenanthe* (mean observed count per square = 1.06, MAE = 0.01, across 86 squares), to errors of nearly two individual birds for species such as meadow pipit *Anthus pratensis* (mean observed count per square = 13.31, MAE = 1.99, across 319 squares; Table 3). This result was robust to cross-validation for the majority of species (Table S2), indicating that biodiversity-habitat associations produced without detailed habitat data may result in significantly suboptimal recommendations for environmental management. Potential implications of the disparity in assessment accuracy extend to further applications such as predictions of effects of climate (Foley *et al.* 2005), policy change (Mattison & Norris 2005) and Environmental Impact Assessments (Treweek 1996).

Widespread declines in biodiversity (Butchart *et al.* 2010) and growing pressures on land use (Foley *et al.* 2005) are increasing demand for large-scale data on land-use and biodiversity for policy and environmental management. The strength of our analyses relates to the novel combination of a large geographic scale with fine-grained observation of Landscape Features and national monitoring methods for estimating bird populations from a random sample of countryside. The results of this study suggest that investment in future analyses should consider the scale and detail required to optimise understanding of biodiversity-habitat associations, and produce better-informed environmental management. The results offer a baseline against which performance of remote-sensing can be assessed as advances in technology improve the resolution (in terms of spatial grain and habitat classification) and accuracy of the data produced.

Broad Habitats provided more reliable predictions than Landscape Features, across the 60 species tested. This may be because Broad Habitats integrate multiple habitat characteristics over larger areas (Benton, Vickery & Wilson 2003), while Landscape Features reflect more specific habitat features, as well as being correlated with basic land cover (Siriwardena, Cooke, & Sutherland 2011). Models combining both Broad Habitats and Landscape Features performed better than either type alone, regardless of the source (field survey or remote-sensing) of Broad Habitat data. This suggests possibilities for enhancement of national monitoring of breeding birds. Wildlife surveys collecting additional detail on landscape features (length of linear features, counts of point ones), for combination with available remote-sensed data, may benefit understanding of large scale biodiversity-habitat associations. Although Broad Habitats were found to outperform Landscape Features, no attempt was made to control the number of input variables from the two that were included in any given model. Overall, a mean of 6.07 Broad Habitat predictors were included per species, higher than the mean of 3.13 Landscape Feature predictors included per species (Table S1). Studies focussed on the roles of these two habitat variable types should test their relative benefits explicitly with adequate controls (Siriwardena, Cooke, & Sutherland 2011).

Landscape Features (e.g. woody linear features, individual trees, scrub, rivers, streams, stone walls, ditches, fences, banks, ponds) can have important effects (positive or negative) on many species by providing sources of food, nest sites or protection from/exposure to predators (Fuller 2012). As such, measures of Landscape Features are important from the perspective of applied management. Habitats impact bird abundance at multiple scales simultaneously and the context within which a given habitat occurs may influence suitability for breeding birds (Benton, Vickery & Wilson 2003). Broad Habitats may determine basic breeding suitability of an area for a given species (e.g. yellowhammer *Emberiza citrinella* – arable specialist), while Landscape Features may provide resources making them an important determinant of breeding abundance of a species within the habitat matrix (e.g. yellowhammer - trees and hedges, Whittingham *et al.* 2005). Therefore, to predict land-use impacts on biodiversity, simultaneous consideration of all habitat effects is required.

Field survey, but not remote-sensing, recorded Landscape Features in the present study (Fuller *et al.* 2002; Howard *et al.* 2003), but their impact on model performance suggests that future surveys aiming to inform biodiversity-habitat associations, both field survey and remote-sensing, should aim to record both Broad Habitats and Landscape Features. Where pragmatism favours collection of either Broad Habitat or Landscape Feature data but not both (due to limits on survey complexity or time, e.g. as part of 'citizen science' data protocols), Broad Habitats should typically be prioritised. Remote-sensed Broad Habitat data may often be relatively accessible (Shirley *et al.* 2013; Shereen, Bonthoux & Balent 2014) and under such circumstances field survey efforts might best prioritise Landscape Features to be used in combination. This may change in the future if remote-sensed Landscape Feature data are developed (Tebbs & Rowland 2014). Combinations of remote-sensed data and field survey have previously yielded important results in attempts to identify land use impacts on biodiversity (Fuller *et al.* 1998; Nagendra & Gadgil 1999; Saveraid *et al.* 2001). While the best performance was yielded by the using both Broad Habitats and Landscape Features from field survey, our results suggest that the performance benefits lost by using remote-sensed Broad Habitats combined with field survey Landscape Features might be outweighed by potential cost reductions under some circumstances (Fig. 1, Fig. 2, Table 2).

The extra performance yielded by field data may be due to greater resolution (in terms of both spatial grain and habitat classification) and accuracy compared with remote-sensing. Broad Habitat areas were more accurately mapped by field survey (minimum mappable unit 20 m^2) than by remote-sensing (pixel-based measures interpreted from satellite images, pixel size 25 m^2, minimum mappable unit > 50 m^2) and Broad Habitat classification was more accurate by field survey (survey based on plant species composition) than remote-sensing (computer-based interpretation of satellite land cover image reflectance) (Fuller *et al.* 2002; Howard *et al.* 2003). Remote-sensing technology has developed since the data were collected, with resolution, scale, accuracy and availability of data increasing (Recio *et al.* 2013, Shirley *et al.* 2013); for example, the Land Cover Map for 2007 incorporates an Ordnance Survey polygon framework to improve habitat mapping (Morton *et al.* 2011). However, the breadth of habitat classification and pixel size, key differentials with field data, remain the same. The ability of remote-sensed data to predict bird abundance is likely to improve with technological advancements.

Addressing the relative costs of field survey and remote-sensing methods is an important issue. Countryside Survey 2007 field survey cost £4.1M for a randomly stratified sample of squares, whilst Land Cover Map 2007 cost £1.8M for all GB squares. Field data benefits therefore come at an increased cost of approximately 128%. However, cost measurement for either field survey or remote-sensing is not straightforward. For field survey, mapping comprises just one element of the survey (besides soils, freshwaters and extensive vegetation sampling). For remote-sensing, many development costs involved in early surveys may not be incurred in the future. Therefore, these costs do not necessarily represent accurate costs for future surveys.

Technological developments are increasing data quality yielded by both field survey and remote-sensing, whilst reducing costs. Advances in field data collection efficiency have occurred in parallel with those in remote-sensing and we estimate that an average of 2 person days are required to collect detailed field data from a 1 km square using Countryside Survey field protocols, which are then available for immediate analysis. Methods such as lidar offer possibilities for improving the resolution of remote-sensed data, but costs associated with this method are considerably higher than those of satellite data and processing costs for data at national scales are currently likely to be prohibitive (Mason *et al.* 2003; Turner *et al.* 2003, Müller & Brandl 2009). The remote-sensed data in this study recorded land cover for the whole of Great Britain, while the field survey was limited to sample 1 km squares. One important consequence of this extra spatial coverage from remote-sensing is that it allows out-of-sample predictions beyond bird survey areas. As the area of interest for a study increases, the cost of field survey would increase relative to the cost of remote-sensing and at some threshold outweigh any benefit (given that funding of field surveys of the entire land surface of Great Britain seems implausible) (Blackburn & Gaston 2002). The threshold scale at which this shift occurs may be reduced if developments in the resolution and cost efficiencies of remote-sensing outstrip equivalent developments in field survey. As the resolution, accuracy and relative costs of remote-sensing and field survey methods develop, further comparisons should be made to measure progress in biodiversity-habitat associations to inform policy decision regarding allocation of research funding. Such comparisons should consider a range of taxa due to the varying importance of resolved information for different organisms.

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Data Accessibility

Countryside Survey & Land Cover Map: Countryside Survey and Land Cover Map data are publicly accessible via http://countrysidesurvey.org.uk/. Due to confidentiality of location data, spatial information is available subject to a licence agreement. Details are available here: http://countrysidesurvey.org.uk/data-access

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Table 1. Five *'Model Types'* differing in the origin of habitat predictors used

Five *'Model Types'* (each applied to all 60 bird species) were produced. *'Model Types'* varied based upon inclusion of predictors from Broad Habitats, Landscape Features or Combined Habitats (both Broad Habitats and Landscape Features) and also based on the data source of Broad Habitats (field data or remote-sensed). Landscape Features were sourced from field data only. NA = Not applicable.

Model Type Name	Landscape Feature Data Source	Broad Habitat Data Source
Field Data Landscape Features	Field Data	NA
Remote-sensed Broad Habitats	NA	Remote-sensed
Field Data Broad Habitats	NA	Field Data
Remote-sensed Combined Habitats	Field Data	Remote-sensed
Field Data Combined Habitats	Field Data	Field Data

Table 2. Summary of seven comparisons between *'Model types' testing two main hypotheses of habitat data performance in prediction of bird abundance*

Hypothesis (the hypothesis of interest), Comparison (the *'Model type'* comparisons aimed at testing each hypothesis), Model type 1 & 2 (the two 'Model Types' being compared, see Table 2), Best performance (the result of the comparison, which of the two sets being compared performed best in prediction of bird abundance), Test Statistic (estimated mean difference in explanatory power, measured as percent deviance explained, across 60 bird species). C.I. (bootstrapped 95 % Confidence Interval), p (bootstrapped p-value), Lower model % (explanatory power of the lower performing model from the comparison as a percentage of the explanatory power of the better performing model from the comparison).

Hypothesis	Model Type 1	Model Type 2	Best Performance	Test Stat	C.I. 2.5%	C.I. 97.5%	p	Lower model %
Field Data versus Remote-sensed	Field Data Combined Habitats	Remote-sensed Broad Habitats	**Field Data**	8.86	-2.67	2.95	< 0.001	73
	Field Data Broad Habitats	Remote-sensed Broad Habitats	**Field Data**	3.89	-1.84	1.84	< 0.001	86
	Field Data Combined Habitats	Remote-sensed Combined Habitats	**Field Data**	3.91	-1.70	1.66	< 0.001	88
Broad Habitats versus Landscape Features	Field Data Broad Habitats	Field Data Landscape Features	**Broad Habitats**	13.82	-4.25	4.44	< 0.001	50
	Remote-sensed Broad Habitats	Field Data Landscape Features	**Broad Habitats**	9.92	-3.33	3.46	< 0.001	59

Table 3 Comparison of error between fitted and observed values for models based on field data and remote-sensing

Comparing Field Data Combined Habitats (combining Broad Habitat + Landscape Feature predictors) and Remote Sensed Data (Broad Habitat predictors only). Sample size = number of 1km squares used for species-specific analysis. Zeros = number of squares with zero count. Max observed = maximum observed count. Mean observed = mean observed count. MAE = mean absolute error between fitted and observed values. Scaled MAE = MAE divided by mean count for species. Values in bold indicate smaller error for Field Data or Remote Sensed Data.

Species	**Sample size**	**Zeros**	**Max observed**	**Mean observed**	**MAE Field Data**	**MAE Remote Sensed**	**Scaled MAE Field Data**	**Scaled MAE Remote Sensed**
Blackbird	328	79	79	8.41	**4.44**	4.84	**0.53**	0.58
Blackcap	256	104	21	2.29	**1.75**	1.82	**0.76**	0.80
BlueTit	305	98	71	6.23	**4.19**	4.63	**0.67**	0.74
Bullfinch	271	202	6	0.45	**0.58**	0.60	**1.30**	1.34
Buzzard	232	99	9	1.24	**1.08**	1.11	**0.87**	0.89
Carrion Crow	335	80	69	6.74	**7.59**	8.45	**1.13**	1.25
Chaffinch	322	51	72	13.51	**1.53**	1.67	**0.11**	0.12
Chiffchaff	262	144	22	1.63	**1.22**	1.31	**0.75**	0.81
Coal Tit	297	189	21	1.15	**1.63**	1.80	**1.42**	1.56
Collared Dove	260	164	23	1.70	5.55	**5.54**	3.26	3.26
Cuckoo	308	208	6	0.54	**0.67**	0.68	**1.25**	1.28

Curlew	255	169	53	1.85	**2.26**	2.35	**1.22**	1.27
Dunnock	310	108	22	2.87	**1.98**	2.11	**0.69**	0.73
Garden Warbler	241	174	9	0.53	**0.69**	0.70	**1.31**	1.33
Goldcrest	295	163	23	1.91	**1.70**	1.83	**0.89**	0.96
Goldfinch	273	109	21	2.71	**2.21**	2.33	**0.82**	0.86
G.S. Woodpecker	255	169	7	0.58	**0.56**	0.62	**0.96**	1.06
Great Tit	305	114	40	3.27	**2.18**	2.26	**0.67**	0.69
Greenfinch	284	128	31	3.48	**2.89**	3.10	**0.83**	0.89
Green Woodpecker	192	132	15	0.72	0.83	0.83	1.16	1.16
Grey Heron	296	252	92	0.73	1.24	1.24	1.71	1.71
Herring Gull	172	125	200	4.84	**6.23**	7.25	**1.29**	1.50
House Martin	292	187	417	4.06	5.71	**5.51**	1.41	**1.36**
House Sparrow	308	156	99	5.65	**5.24**	5.51	**0.93**	0.98
Jackdaw	280	119	107	6.90	**7.12**	7.14	**1.03**	1.04
Jay	222	155	20	0.65	**0.70**	0.72	**1.08**	1.10
Kestrel	304	218	3	0.35	**0.44**	0.46	**1.29**	1.32
Lapwing	290	214	71	1.97	**2.78**	2.83	**1.41**	1.44
Linnet	264	127	41	3.80	**3.88**	3.96	**1.02**	1.04

Long Tailed Tit	269	180	22	1.35	**1.40**	1.59	**1.04**	1.18
Magpie	240	88	30	3.21	**2.65**	2.84	**0.83**	0.89
Mallard	322	193	31	2.22	**2.54**	2.67	**1.14**	1.20
Meadow Pipit	319	117	202	13.31	**9.34**	11.33	**0.70**	0.85
Mistle Thrush	302	160	11	1.26	**1.26**	1.29	**1.00**	1.02
Moorhen	239	185	10	0.53	**0.65**	0.74	**1.23**	1.40
Nuthatch	167	117	24	0.84	0.93	**0.91**	1.10	**1.08**
Oystercatcher	199	132	24	2.07	**2.49**	2.76	**1.20**	1.33
Pied Wagtail	329	143	10	1.53	**1.30**	1.33	**0.85**	0.87
Raven	163	112	8	0.69	0.90	**0.89**	1.30	**1.28**
Reed Bunting	266	205	15	0.73	**0.80**	0.98	**1.11**	1.35
Robin	322	65	49	7.79	**4.60**	5.23	**0.59**	0.67
Sedge Warbler	222	170	25	1.21	**1.32**	1.69	**1.09**	1.39
Siskin	179	127	13	1.07	**1.13**	1.19	**1.05**	1.12
Skylark	332	102	87	6.92	**5.85**	6.30	**0.85**	0.91
Snipe	244	201	35	0.49	**0.59**	0.70	**1.20**	1.42
Song Thrush	323	105	20	2.72	**1.93**	2.06	**0.71**	0.76
Sparrowhawk	277	234	2	0.18	0.26	**0.25**	1.46	**1.42**

Starling	315		156	380		10.57	11.20	**10.56**	1.06	**1.00**
Stock Dove	235		158	12		0.94	**1.16**	1.19	**1.23**	1.26
Stonechat	146		96	12		1.05	**0.94**	1.26	**0.90**	1.20
Swallow	320		91	34		5.38	**3.69**	4.00	**0.69**	0.74
Swift	267		172	120		2.74	**3.56**	3.66	**1.30**	1.34
Treecreeper	277		220	5		0.32	**0.42**	0.45	**1.31**	1.40
Tree Pipit	232		182	14		0.62	0.77	0.77	**1.23**	1.25
Wheatear	248		162	16		1.06	**1.13**	1.14	**1.06**	1.08
Whitethroat	262		131	20		2.00	**1.77**	1.89	**0.89**	0.94
Willow Warbler	323		104	49		6.34	**4.91**	5.13	**0.78**	0.81
Woodpigeon	309		82	108		13.72	**9.86**	10.01	**0.72**	0.73
Wren	335		48	47		10.39	**5.47**	6.50	**0.53**	0.63
Yellowhammer	260		131	20		2.39	**1.88**	1.98	**0.79**	0.83
		Mean	2.76	2.94	1.04	1.11				

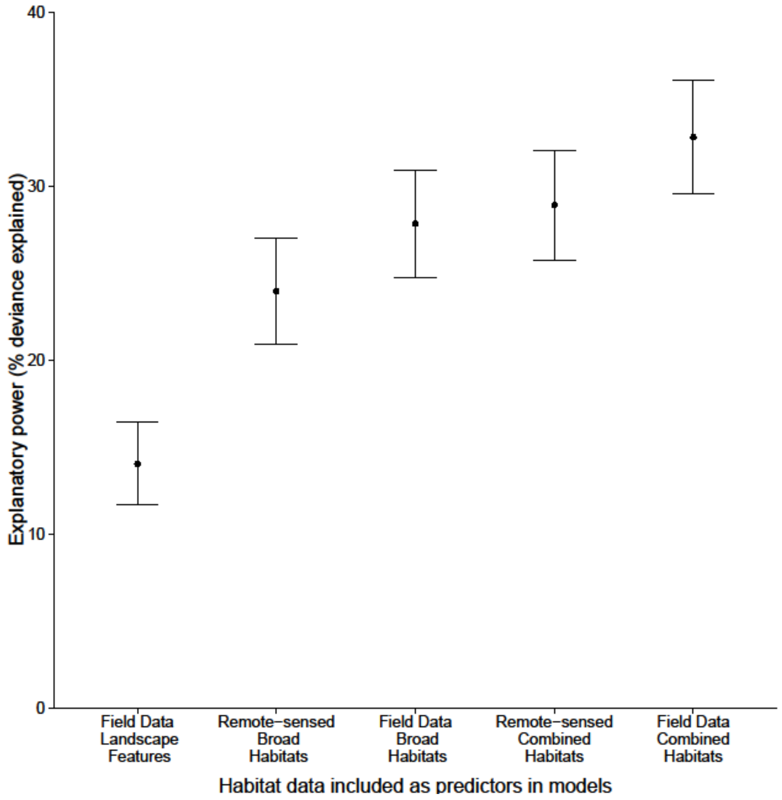

Figure 1. Mean explanatory power (± 95% Confidence Interval) across 60 bird species for five *'Model Sets'* generated from field data and remote-sensed data

'*Field Landscape'* = Landscape feature predictors from field data. '*Remote Broad Habitat*' = Broad Habitat predictors from remote-sensed data. '*Field Broad Habitat*' = Broad Habitat predictors from field data. '*Remote Combined*' = Broad Habitat predictors from remote-sensed data + Landscape Features from field data, '*Field Combined*' = Broad Habitat predictors from field data + Landscape Features from field data. Significant differences: Field Landscape versus Field Broad Habitat/Remote Broad Habitat/Field Combined ($p < 0.001$), Remote Broad Habitat versus Field Broad Habitat/Remote Combined/Field Combined ($p < 0.001$), Field Broad Habitat versus Field Combined ($p < 0.001$), Remote Combined versus Field Combined ($p < 0.001$), (Table 2).

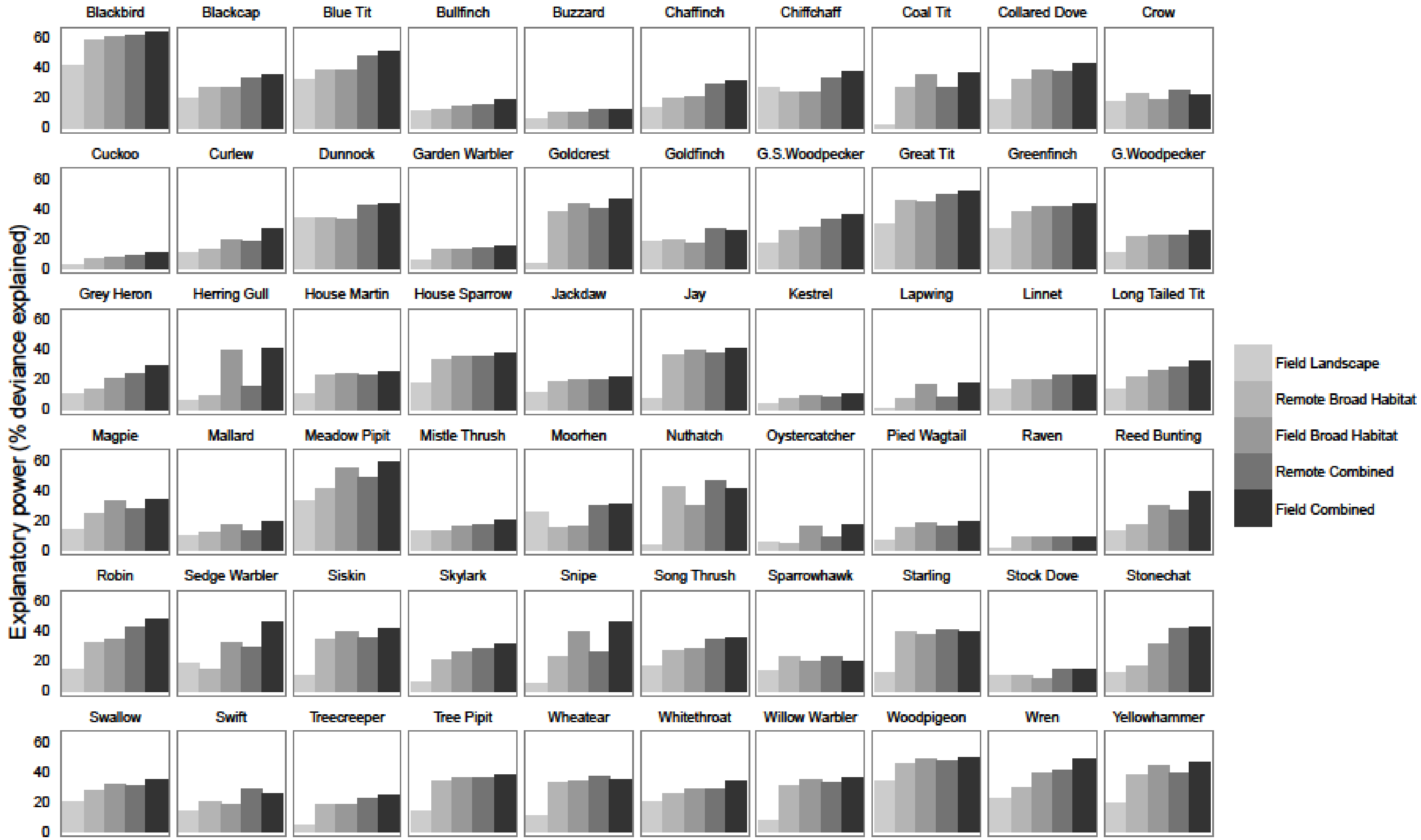

Figure 2. Explanatory power for 60 individual bird species models generated from field data and remote-sensed habitat predictors

'*Field Landscape'* = Landscape Feature predictors from field data (Countryside Survey). '*Remote Broad Habitat*' = Broad Habitat predictors from remote-sensed data (Land Cover Map). '*Field Broad Habitat*' = Broad Habitat predictors from field data. '*Remote Combined*' = Broad Habitat predictors from remote-sensed data + Landscape Features from field data, '*Field Combined*' = Broad Habitat predictors from field data + Landscape Features from field data.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Bird species, sample sizes and habitat predictors included in hypotheses

Table S2 Comparison of error between fitted and observed values for models based on field data and remote-sensing in out-of-sample prediction